

SYSTEMATICS AND BIOLOGY OF THE BONEFISH, *ALBULA NEMOPTERA* (FOWLER)¹

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ABSTRACT

This study is a review of the taxonomic status of the bonefish, *Albula nemoptera*, formerly placed in the genus *Dixonina*. Reasons for synonymizing *Dixonina* with *Albula* are discussed, and it is shown that *pacifica* is conspecific with *nemoptera*. The Atlantic and Pacific populations of

nemoptera are compared with each other and with the common bonefish, *A. vulpes*. Presumed larval and juvenile stages of *nemoptera* are described and compared with those of *vulpes*. The ecology and distribution of *nemoptera* and *vulpes* is discussed.

Prior to 1911 the family Albulidae was known from several fossil forms and one living species, *Albula vulpes* (Linnaeus). Fowler (1911) described the second living species, *Dixonina nemoptera*, from a single specimen from Hispaniola. Eight years later a second specimen was recorded by Metzelaar (1919) from Venezuela and a third, from the Pacific coast of Mexico, by Myers (1936). A drawing of a specimen from the Pacific coast of Mexico identified as "*Albula vulpes*," was published by Kumada and Hiyama (1937). According to Walford (1939), apparently several specimens were available to these authors. Beebe (1942), on the basis of 19 specimens from Costa Rica, proposed the name "*Dixonina pacifica*" for the Pacific coast population. The third Atlantic record (Rivas, 1952) was based on two specimens from Jamaica. Recently Caldwell and Caldwell (1964) recorded, tentatively as "*Albula vulpes*," 14 larvae and juveniles from the Atlantic coast of Panama.

According to the literature, therefore, this apparently rare species of albulid was hitherto known only from four Atlantic records (7 larvae, 6 juveniles, and 4 adults) and the three Pacific records (21 specimens of which 14 are not traceable).

During its cruise No. 92, May 5 through June 17, 1964, the Bureau of Commercial Fisheries exploratory fishing vessel *Oregon* collected 21 adult specimens of *Albula nemoptera* along the Atlantic coast of Colombia. Nineteen of these are available for the present study (see materials and acknowledgments); one was deposited at the Santa Marta Marine Laboratory, Santa Marta, Colombia, and another at the Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory in Miami, Fla.

Additional specimens from the Atlantic and Pacific, not previously reported in the literature, were located in various institutions.

The fairly adequate material of *A. nemoptera*, now at hand, prompted this study, particularly because the most recent account of the species was based on a single specimen (Hildebrand, 1963) and the conclusions reached therein are open to question (Berry, 1964). In due fairness to the late S. F. Hildebrand, however, it should be remembered that his study was published 14 years after his death in 1949.

We performed this research at the Bureau of Commercial Fisheries Exploratory Fishing and Gear Research Base, Pascagoula, Miss.

MATERIALS

This paper is based on 56 specimens (35 Atlantic; 21 Pacific) of *A. nemoptera* and 43 Atlantic specimens of *A. vulpes* from the

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collections of the U.S. National Museum (USNM), Stanford University (SU), Field Museum of Natural History, Chicago (FMNH), Los Angeles County Museum (LACM), University of California at Los Angeles (UCLA), University of Miami Institute of Marine Science (UMML), and University of Miami Ichthyological Museum (UMIM). This material is distributed as follows:

A. nemoptera (Atlantic).—Colombia: about 40 km. (22 nautical miles) NW. of Punta San Bernardo, USNM 199530 (3 adults), FMNH 66796 (2 adults); about 22 km. (12 nautical miles) WNW. of Puerto Colombia, USNM 199474 (6 adults), UMIM 5926 (2 adults); about 23 km. (13 nautical miles) NE. of Santa Marta, FMNH 66795 (2 adults), UMIM 5927 (2 adults); about 18 km. (10 nautical miles) WSW. of Puerto Colombia, UMIM 5925 (2 adults). Panama: Caledonia Bay, LACM 20467 (7 larvae, 4 juveniles), LACM 20468 (2 juveniles). Jamaica: Port Antonio, LACM 5802 (1 adult), UMIM 1028 (2 adults).

A. nemoptera (Pacific).—Mexico: Guerrero, Acapulco, USNM 75547 (1 adult); Sinaloa, Mazatlan Playa Camaron, UCLA W51-22 (13 young). Costa Rica: Potrero Grande, SU 46385 (5 young to adult); Gulf of Nicoya, Quepos, UCLA W54-55 (1 adult). Panama: Perlas Islands, Isla del Rey, Punta de Cocos, UCLA W53-285 (1 young).

A. vulpes (Atlantic). — Florida: Monroe Co., Flamingo, Buttonwood Canal bridge, UMML 16775 (20 young); Dade Co., Miami, UMIM 5917 (2 adults). Bahamas; Cay Sal Bank, Cotton Cay, UNIM 5916 (7 adults). Cuba: Havana, estuary of Guanabo River, UMIM 758 (5 juvenile and young). Jamaica: Port Antonio, UMIM 5918 (1 adult). Colombia: St. Andrews Island, UMIM 5928 (8 larvae).

METHODS

Measurements and counts were made according to methods described by the senior author (Rivas, 1960) with the following modifications and additions. Standard length was measured from the tip of the snout (not the upper lip) to the middle of the caudal base. Prepectoral length was measured from the tip of the snout

to the insertion of the appressed left pectoral fin. Head length is the longest distance between the tip of the snout and the margin of the left opercular membrane. Mandible length comprises the distance between the anterior tip of the dentary and the posterior tip of the left articular. Preoral length is the median ventral distance between the tip of the snout and the anterior tip of the dentary with the mouth closed. Body depth was measured at the origin of the dorsal fin. Dorsal and anal fin heights were measured from the origin of the erect fin to the upper tip. Last dorsal and last anal ray lengths were measured between the end of the fin base and the tip of the ray. All the dorsal and anal rays were counted, including the anteriormost short, closely approximated elements. The last two dorsal and anal rays were counted separately. All counts were made from the fish's left side. All pectoral and pelvic rays and all branched caudal rays were counted. All pored scales were counted including those beyond the caudal base. The scales above the lateral line were counted downward and backward from the dorsal fin origin to, but not including, the lateral line. Those below the lateral line were counted upward and forward from the anal fin origin to, but not including, the lateral line. Only the modified predorsal scales, along the midline of the back anterior to the dorsal fin, were counted. The scales around the caudal peduncle were counted at the region of the least depth. All the gill rakers on the first arch were counted, including rudiments; the count for the lower limb includes the gill raker at the angle. All branchiostegal rays were counted. The vertebral counts include the hypural.

GENERIC STATUS OF THE BONEFISH

Largely on subjective grounds the genus *Dixonina* Fowler (1911) is here considered as a synonym of the genus *Albula* Scopoli (1777).

The only two living species of the family Albulidae (*Pterothrissus* not included), *A. vulpes* and *A. nemoptera*, are much more closely related to each other than previously suspected. The differences between them are only of degree and not of the order that would merit generic separation (tables 1-11). Their great superficial similarity is further emphasized by

TABLE 1.—Comparison of 21 Atlantic *Albula nemoptera* and 10 *A. vulpes* of similar mean length on the basis of differential proportional characters (in thousandths of the standard length)

[Ontogenetic variation of characters is indicated by symbols in parentheses: (I) isometric, (A+) positively allometric, (A-) negatively allometric]

Character	<i>A. nemoptera</i>		<i>A. vulpes</i>	
	Range	Mean	Range	Mean
Standard length (mm.)	234-341	289	304-387	293
Prepectoral length (A-)	270-301	286	255-290	268
Precaudal length (A+)	824-847	836	835-856	844
Head length (I)	289-312	299	267-296	286
Maxillary length (I)	133-142	138	91-103	94
Mandible length (I)	118-128	123	83- 97	93
Preoral length (I)	43- 49	46	26- 35	29
Orbit diameter (I)	46- 53	50	52- 60	55
Caudal peduncle depth (I)	60- 68	63	70- 78	74
Dorsal base length (I)	173-190	183	138-176	154
Dorsal fin height (A-)	161-177	169	182-197	188
Last dorsal ray length (A+)	152-193	170	54- 56	60
Last anal ray length (A+)	80- 99	89	54- 65	58
Upper caudal lobe length (A-)	204-234	223	232-275	256
Lower caudal lobe length (A-)	187-208	200	216-254	239

TABLE 2.—Comparison of 9 Atlantic and 7 Pacific specimens of *Albula nemoptera* of similar mean length on the basis of proportional characters (thousandths of the standard length)

[Ontogenetic variation of characters is indicated by symbols in parentheses: (I) isometric, (A+) positively allometric, (A-) negatively allometric]

Character	Atlantic		Pacific	
	Range	Mean	Range	Mean
Standard length (mm.)	72-341	246	78-346	205
Predorsal length (A+)	464-490	479	473-513	489
Prepectoral length (A-)	278-301	288	267-294	283
Prepelvic length (A+)	558-602	589	570-610	586
Preoral length (A+)	806-847	829	814-838	830
Head length (I)	297-304	300	289-302	290
Snout length (I)	110-120	115	107-116	111
Maxillary length (I)	133-140	138	124-139	130
Mandible length (I)	119-128	123	111-129	118
Preoral length (I)	43- 49	45	39- 49	42
Orbit diameter (A-)	47- 68	53	46- 67	52
Interorbital width (I)	61- 69	65	61- 66	65
Body depth (A+)	178-199	190	165-208	184
Caudal peduncle depth (I)	60- 70	65	62- 68	66
Dorsal base length (I)	179-194	186	181-204	189
Anal base length (I)	51- 63	58	56- 66	59
Dorsal fin height (A-)	163-192	173	171-194	184
Anal fin height (I)	87- 94	90	88-105	98
Pectoral fin length (I)	142-152	147	141-161	151
Pelvic fin length (I)	114-136	121	120-130	125
Last dorsal ray length (A+)	39-178	150	45-175	130
Last anal ray length (A+)	49- 96	86	54-107	87
Upper caudal lobe length (A-)	204-234	222	217-237	237
Lower caudal lobe length (A-)	187-208	200	212-230	222

TABLE 3.—Frequency distribution of dorsal and pelvic rays in *Albula nemoptera* and *A. vulpes*

Species	Dorsal rays						Pelvic rays				
	No.	18	19	20	21	Mean	8	9	10	11	Mean
<i>A. nemoptera</i> (Atlantic)	28			3	25	20.9		28			9.0
<i>A. nemoptera</i> (Pacific)	21			4	17	20.8	1	20			9.0
<i>A. vulpes</i> (Atlantic)	39	10	29			18.7		3	35	1	9.9

TABLE 4.—Frequency distribution of pectoral rays in *Albula nemoptera* and *A. vulpes*

Species	Pectoral rays						
	No.	15	16	17	18	19	Mean
<i>A. nemoptera</i> (Atlantic)	28		3	22	3		17.0
<i>A. nemoptera</i> (Pacific)	21	2	4	10	4	1	16.9
<i>A. vulpes</i> (Atlantic)	35			2	20	13	18.3

TABLE 5.—Frequency distribution of lateral line scales in *Albula nemoptera* and *A. vulpes*

Species	Lateral line scales																				
	No.	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	Mean
<i>A. nemoptera</i> (Atlantic)	22											1	4	5	5	4	2				81.5
<i>A. nemoptera</i> (Pacific)	17												2	1	2	5	4	2		1	82.1
<i>A. vulpes</i> (Atlantic)	38	1	1	3	6	8	9	3	3	2	2										72.6

TABLE 6.—Frequency distribution of scales above and below lateral line, and around caudal peduncle in *Albula nemoptera* and *A. vulpes*

Species	Scales above lateral line				Scales below lateral line				Scales around caudal peduncle				
	No.	8	9	10	Mean	6	7	8	Mean	16	17	18	Mean
<i>A. nemoptera</i> (Atlantic)	22	18	4	9	2	7	15	7	7	19	3		16.1
<i>A. nemoptera</i> (Pacific)	19	14	4	9	2	6	13	7	7	11	7	1	16.5
<i>A. vulpes</i> (Atlantic)	37	5	30	2	8.9	32	5		6.1	37			16.0

TABLE 7.—Frequency distribution of predorsal scales in *Albula nemoptera* and *A. vulpes*

Species	Predorsal scales												
	No.	13	15	16	17	18	19	20	21	22	23	24	Mean
<i>A. nemoptera</i> (Atlantic)	22				1	3	2	7	8	1			20.0
<i>A. nemoptera</i> (Pacific)	16				4	2	4	5	1				19.8
<i>A. vulpes</i> (Atlantic)	29	2		6	8	4	1	1	2	3	1	1	18.1

TABLE 8.—Frequency distribution of lower and upper limb gill rakers in *Albula nemoptera* and *A. vulpes*

Species	Lower limb						Upper limb								
	No.	9	10	11	12	13	Mean	5	6	7	8	9	10	11	Mean
<i>A. nemoptera</i> (Atlantic)	28	6	18	4			9.9	2	11	6	3	5	1		7.0
<i>A. nemoptera</i> (Pacific)	21	4	9	8			11.2			7	8	5	1		9.0
<i>A. vulpes</i> (Atlantic)	39			8	27	4	11.9			10	19	5	3	2	8.2

TABLE 9.—Frequency distribution of total gill rakers in *Albula nemoptera* and *A. vulpes*

Species	Total gill rakers										Mean
	No.	15	16	17	18	19	20	21	22	23	
<i>A. nemoptera</i> (Atlantic).....	28	4	8	7	4	3	2	---	---	---	17.0
<i>A. nemoptera</i> (Pacific).....	21	---	---	---	1	5	7	6	1	1	20.2
<i>A. vulpes</i> (Atlantic).....	39	---	---	---	3	9	16	8	2	---	20.0

TABLE 10.—Frequency distribution of branchiostegal rays in *Albula nemoptera* and *A. vulpes*

Species	Branchiostegal rays								Mean
	No.	10	11	12	13	14	15	16	
<i>A. nemoptera</i> (Atlantic).....	27	---	---	---	14	11	2	---	13.6
<i>A. nemoptera</i> (Pacific).....	21	---	---	---	4	12	5	---	14.0
<i>A. vulpes</i> (Atlantic).....	39	7	11	14	6	1	---	---	11.6

TABLE 11.—Frequency distribution of vertebrae in *Albula nemoptera* and *A. vulpes*

Species	Vertebrae											Mean		
	No.	69	70	71	72	73	74	75	76	77	78		79	80
<i>A. nemoptera</i> (Atlantic).....	20	---	---	---	---	---	---	---	---	3	7	10	---	78.4
<i>A. nemoptera</i> (Pacific).....	20	---	---	---	---	---	---	---	---	1	9	9	1	78.5
<i>A. vulpes</i> (Atlantic).....	20	10	10	---	---	---	---	---	---	---	---	---	---	69.5

a comparison of their detailed structures. From the characters studied there is more indication of similarity than divergence. The most important differences between the two species are the larger mouth and the longer last dorsal and anal rays in *A. nemoptera*. Other differences were in dentition, certain proportions, meristic characters, and color markings.

Even their ancestry, as reconstructed from fossil material, indicates that *A. vulpes* and *A. nemoptera* should not be considered as representing separate monotypic genera. Frizzell (1965), after studying otoliths, suggested a phylogeny of albulid genera dating back to the Cretaceous. Although he retained *Albula* and *Dixonina* as separate genera, his illustrations, descriptions, and comments indicate that these two genera are more closely related to each other than either is to any of their predecessors. Both *Albula* and *Dixonina* are tentatively shown by Frizzell to be descended from the Eocene-Oligocene genus *Metalbula* Frizzell.

Radiographs of 20 juvenile to adult *A. vulpes* and 40 juvenile to adult *A. nemoptera* indicate

that the otolith (sagitta) of *A. vulpes* is more inclined, with respect to the axis of the vertebral column, than that of *A. nemoptera*. This has been confirmed by Don L. Frizzell (personal correspondence).

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Dixonina nemoptera Fowler, 1911; 652 (original description); Santo Domingo, West Indies. Myers, 1936: 83–85 (new record; compared with *Albula*; Acapulco, Mexico). Walford, 1939: 119 (identification of drawing from Kumada and Hiyama, 1937; Gulf of California). Beebe, 1942: 45 (compared with *D. pacifica*). Rivas, 1952: 3 (popular account of new record; Port Antonia, Jamaica). Hildebrand, 1963: 143–145 (description; relationship; range; synonymy; Acapulco, Mexico). Caldwell and Caldwell, 1964: 4 (dorsal fin rays; Jamaica). Berry, 1964: 722 (synonymy with *D. pacifica* questioned). Frizzell, 1965: 85 (otolith-based taxonomy, classification, lineage, paleoecology).

Albula nemoptera Metzelaar, 1919: 9 (description; comments; generic separation not justified; Puerto Cabello, Venezuela).

Albula vulpes (not of Linnaeus) Kumada and Hiyama, 1937: (colored plate; Gulf of California). Caldwell and Caldwell, 1964: 4–5 (dorsal fin rays; tentative identification; Caledonia Bay, Panama).

Dixonina pacifica Beebe, 1942: 43 (original description; compared with *D. nemoptera*; Potrero Grande, Culebra Bay, and Piedra Blanca, Costa Rica). Hildebrand, 1963: 144–145 (synonymized with *D. nemoptera*; Acapulco, Mexico). Berry, 1964: 722 (synonymy with *D. nemoptera* questioned).

A comparison of specimens from the Atlantic and the Pacific Oceans (tables 2 to 11) indicates that *pacifica* should not be considered as specifically distinct from *nemoptera*. No significant differences were found in 18 of the 23 proportional characters studied (table 2). In the five characters that show differences (dorsal and anal fin height, last dorsal ray length, upper and lower caudal lobe length) the overlap is quite broad. Tables 3 to 11 show that meristic characters are about the same in the Atlantic and Pacific populations with the

exception of the apparent higher number of gill rakers (tables 8 and 9) in the Pacific population. This exception results from the indistinction of the anterior one or two rakers in the larger specimens because of encroachment by the surrounding spinous areas. The Pacific specimens were smaller than those from the Atlantic by an average of 69 mm.; this is about one-fifth of the largest Atlantic (341 mm.) and the largest Pacific (346 mm.) specimens available. In spite of the apparent difference in the number of gill rakers between the Atlantic and Pacific populations, the overlap is broad and the mean difference small. The Atlantic and Pacific populations do not differ in other characters studied, as discussed below. The number of anal rays (9) not shown in the tables is constant in the Atlantic and Pacific populations.

The Atlantic and Pacific populations of *A. nemoptera* appear to differ slightly in the height of the dorsal and anal fins, the length of the last dorsal ray, the length of the caudal lobes, and the number of gill rakers. These differences, however, do not justify separation at the species level and, probably, not even at the subspecies level. The alleged differences described by Beebe (1942) all break down when adequate material is analyzed.

The following is an itemized description of qualitative characters.

Heart.—The heart of one adult Atlantic specimen was dissected. It has two rows of valves in the conus as in *A. vulpes*.

Gular plate.—Hildebrand (1963: 132), the last reviewer, and most preceding authors, stated that a gular plate is absent in the family Albulidae; however, Nybelin (1960: 78) has demonstrated its presence in *A. vulpes*. Following Nybelin's method (alizarine stain), we found that *A. nemoptera* has a gular plate, similar to that of *A. vulpes*.

Dentition.—A detailed description of Pacific specimens' dentition was given by Beebe (1942). Atlantic specimens are in full agreement with that description. As indicated by Beebe, there is considerable ontogenetic variation in the teeth.

Coloration.—The life colors, based on Pacific specimens, were described by Beebe

(1942). Two specimens (UMIM 1028) collected in Port Antonio, Jamaica, were in agreement with Beebe's description. Preserved material has longitudinal dark lines, between the rows of scales, especially above the lateral line. There are an elongate black dash anteriorly on each side of the snout and a median anchor-shaped mark on the tip of the snout extending ventrally towards the mouth.

Size.—The largest known specimen from the Atlantic (Colombia, UMIM 5927) is 341 mm. in standard length, and the largest known Pacific specimen (Acapulco, Mexico, USNM 75547) is 346 mm.

Sex ratio.—The 19 Colombian specimens were sexed: 9 mature males and 10 mature females.

Range.—In the Atlantic the species is now known to occur along the Caribbean coasts of Venezuela, Colombia, and Panama, and at Jamaica and Hispaniola. In the Pacific it is known from Mazatlan and Acapulco, Mexico, and from Costa Rica and Panama.

RELATIONSHIPS WITH *ALBULA VULPES*

A. nemoptera and *A. vulpes* differ in several proportional characters, especially those pertaining to mouth structures and to the elongation of the last dorsal and anal rays into a filament in *A. nemoptera* (table 1). These characters, as well as meristic differences (tables 3 to 11) leave no doubt as to the specific distinction between *A. nemoptera* and *A. vulpes*. As already discussed, however, these are differences of degree not to be considered of generic importance. More basic structural characters such as the presence of a gular plate and two rows of valves in the conus arteriosus are common to both species.

Differences in dentition between *A. nemoptera* and *A. vulpes* are, again, of degree. The premaxillary, dentary and palatine teeth are larger in *A. nemoptera*. Also in *A. nemoptera* the premaxillary band of teeth is two or three teeth wide at the symphysis and three or four in *A. vulpes*. The parasphenoid and entopterygoid teeth, however, are larger and fewer in *A. vulpes*. Maxillary teeth are present in juvenile and young adult *A. nemoptera* to about 250 mm. in standard length, whereas maxillary

teeth are present only in juvenile *A. vulpes* less than 50 mm.

The only differences in color pattern between *A. vulpes* and *A. nemoptera* are the markings on the snout. In *A. vulpes* there is a median inverted U-shaped mark on the tip of the snout instead of an anchor-shaped mark and there are no lateral black dashes.

Both species are sympatric, but there is evidence that they may be partially segregated ecologically. This is discussed elsewhere in this study.

For purposes of identification and comparison the most significant differences between *A. nemoptera* and *A. vulpes* are summarized in the following key:

1a.—Vertebrae 77 to 80. Dorsal rays 21, rarely 20. Pelvic rays 9. Pectoral rays 16 to 18, usually 17. Branchiostegal rays 13 or 14, rarely 12 or 15. Lateral line scales 78 to 84, usually 80 to 82. Last ray of dorsal fin prolonged into a filament reaching beyond vertical from tip of pelvic fin (except in specimens smaller than 75 mm. in standard length). Last ray of anal fin prolonged into a filament longer than anal fin base (except in specimens smaller than 75 mm. in standard length). Maxillary reaching beyond vertical from anterior margin of orbit.

..... *Albula nemoptera*

1b.—Vertebrae 69 or 70. Dorsal rays 18 or 19, usually 19. Pelvic rays 10, rarely 9 or 11. Pectoral rays 17 to 19, usually 18. Branchiostegal rays 10 to 14, usually 11 or 12. Lateral line scales 68 to 77, usually 71 to 73. Last ray of dorsal fin not prolonged into a filament reaching beyond vertical from tip of pelvic fin. Last ray of anal fin not prolonged into a filament longer than anal fin base. Maxillary not reaching to vertical from anterior margin of orbit (except in specimens smaller than 70 mm., standard length).

..... *Albula vulpes*

EARLY STAGES OF DEVELOPMENT

Seven larval albulids, collected with four juvenile *A. nemoptera* in Caledonia Bay, Panama (LACM 20467) are tentatively identified as metamorphosing larvae of *A. nemoptera*. This identification was determined by

comparing these larvae (table 12) with as many of *A. vulpes* of equal size as could be found in Alexander (1961). To avoid misinterpretations resulting from slight differences in measuring and counting, six larval *A. vulpes* of comparable size from St. Andrews island (UMIM 5928) were included as a control.

The presumed *A. nemoptera* larvae differ from those of *A. vulpes* in predorsal length, preanal length, and number of myomeres (table 12). These differences are confirmed by the

TABLE 12.—Comparison of metamorphosing larvae of *Albula nemoptera*? and *A. vulpes* of similar size

[Proportions in thousandths of the standard length]

Character	<i>A. nemoptera</i> ?		<i>A. vulpes</i>			
	Caledonia Bay, Panama, LACM 20467 (7 specimens)		Alexander, 1961: 38-40 (8 specimens)		St. Andrews Island, Colombia, UMIM 5928 (6 specimens)	
Standard length (mm.)	Range 58.3-48.8	Mean 51.3	Range 57.0-48.5	Mean 51.4	Range 56.2-48.0	Mean 52.2
Predorsal length	778-815	795	805-830	818	807-825	814
Preanal length	922-971	944	948-980	968	956-975	968
Number of myomeres	69-74	70.8	67-70	67.8	67-69	68.2

comparison of juveniles of *A. vulpes* and *A. nemoptera* (table 13). In both species the number of vertebrae is higher than the observed

TABLE 13.—Comparison of juveniles of *Albula nemoptera* and *A. vulpes* of similar size

[Proportions in thousandths of the standard length]

Character	<i>A. nemoptera</i>		<i>A. vulpes</i>	
	Caledonia Bay, Panama, LACM 20467, 20468 (5 specimens)		Guanabo, Cuba, UMIM 758 (5 specimens)	
Standard length (mm.)	Range 36-49	Mean 43	Range 30-49	Mean 42
Predorsal length	454-467	460	472-490	481
Preanal length	781-793	787	800-817	812
Number of vertebrae	80-81	80.5	72-74	73.0

number of myomeres, and this difference is probably due to the difficulty in discerning the last, very closely approximated myomeres especially in *A. nemoptera*. The apparent greater number of vertebrae in juveniles (table 13) is, on the average, three or four units greater than in adults (table 11) as counted from the radiographs, and this difference may

be explained by the fusion of three or four terminal vertebral centra in adults as pointed out by Hollister (1936).

The presumed leptocephali of *A. nemoptera* are identical to those of *A. vulpes* in general appearance. The juveniles, however, are readily distinguished from those of *A. vulpes* by the much larger mouth. The smallest juvenile *A. nemoptera* (Caledonia Bay, Panama, LACM 20468) was 36 mm. standard length. Four other juveniles from the same general locality (LACM 20467) were 42 to 49 mm.

Alexander (1961) stated that variation in total myomere counts (65 to 72) might indicate subspeciation or even separate species; some of her larvae with 69 or more myomeres may be *A. nemoptera*.

ECOLOGICAL IMPLICATIONS

Frizzell (1965) discussed the ecology and distribution of recent and fossil albulids and suggested that competition between *A. vulpes* and *A. nemoptera* drove the latter to deeper water. This conclusion was based on the study of fossils.

In agreement with the above suggestion all adults (about 200 mm. standard length or larger) of *A. nemoptera* for which capture data are available, were collected in relatively deep water. The 21 *Oregon* specimens (234 to 341 mm.) were collected in trawls in depths of 27 to 110 m. The three Jamaican specimens (197 to 265 mm.) were taken with handline in about 37 m. The Pacific specimens reported by Kumada and Hiyama (1937) were taken by a trawl but no exact depth of capture was given. Of the 19 Pacific specimens reported by Beebe (1942: 44), 5 (220 to 365 mm.) were taken with handline from the ship (*Zaca*) at undetermined depths; the other 14 (80 to 200 mm.) were collected with a seine presumably in shallow water close to the beach.

The senior author has been watching for *A. nemoptera* since 1938, and he has examined hundreds of bonefish in museums and especially in the field throughout southern Florida, the Bahamas, and the Caribbean area. All adult *A. vulpes* came from depths less than 2 m. except one (231 mm., UMIM 5918) taken with three *A. nemoptera* from Jamaica. No speci-

mens of *A. vulpes* were taken with the *Oregon* collections of *A. nemoptera*.

The available evidence suggests that there could be a bathic segregation of adult populations of *A. vulpes* and *A. nemoptera* where the latter occupies the deeper stratum. Overlap in their depth ranges is also suggested, but the depth and width of the overlap zone cannot be determined now.

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